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Seasonal movement of young plaice in the north-east Irish Sea

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Contents

ABSTRACT . . . . . *Page* iv

INTRODUCTION 1

EQUIPMENT AND METHODS 2

GENERAL RESULTS 3
Grading by length and age-group 4
Types of variation along the line of stations 4

MOVEMENTS DURING THE SUMMER PERIOD 6
Finer structure of the offshore summer movement 8
Maturity grading in August 10

POSITION OF THE AGE-GROUPS DURING WINTER 12
Comparison of spread of age-groups 12
Comparison of spread of sexes 14
Discussion 15

REFERENCES 16

APPENDIX 17

Abstract

The inshore movements of plaice were studied from 1951–53 in order to test the assumptions on which earlier marking experiments were based.

Large catches of one-, two- and three-year-old plaice were taken inshore throughout the summer months, and these were graded according to size and age, the largest and oldest being found further offshore, but few fish were caught in the winter. The rate of disappearance of fish during the autumn is shown to be more gradual than the rate at which they reappear in April and May.

There is a general offshore movement of the age-groups during the summer, but when the finer structure of the movement is examined a slight reversal can be seen at the end of May and beginning of June, and a maturity grading is evident in the two- and three-year-old fish in August—the more mature of both sexes tending to be found further offshore.

Inshore, in the winter, the catch is composed mainly of one-year-old fish, and is about one-tenth of the summer level. Those fish which do go offshore are caught over an area extending up to 35 miles in a general south-westerly direction and show no significant difference in dispersion, either by age or sex, during the period from December to February, but by March (although still mainly offshore) the fish do appear to be graded by age in the order that they assume in the inshore region during the summer months.

At the beginning of the winter, during the offshore migration in November, the female plaice seem to move more quickly than the males. In contrast, at the beginning of the summer the three-year-olds disperse more quickly than the younger fish but there is no significant difference in the spread of the sexes.

Seasonal movement of young plaice in the north-east Irish Sea

Introduction

During 1949 and 1950 over 27 000 plaice were marked off the Cumberland coast in a series of experiments designed to answer problems arising out of the pollution of the sea by radioactive effluent from the Windscale factory. In order to answer these problems, some assumptions were made about the inshore movements of plaice which were suggested by the returns from the marking experiments. These assumptions conformed with the general ideas held by previous workers in the subject, who were studying rather more extensive areas, but for various reasons it was not possible, during that period, to confirm that these theories of inshore movements were directly applicable to this restricted area. Certainly these authorities differed on details. For example, Heincke (1905, 1913) and Meek (1914) wrote of immature plaice being zoned according to length, on the German and Northumberland coasts respectively, and reported seasonal periodic migrations offshore. Johnstone (1915) agreed that young plaice in the Irish Sea made these seasonal variations, but he disagreed with the timing of the inshore and offshore movements, in some cases being in direct contradiction. Redeke (1905) found only a progressive offshore migration on the Dutch coast. However, this paper is not intended to provide a synopsis of previous literature on plaice movement. Wimpenny (1953) published a comprehensive review of the information available from these and most other sources up to that date. Clearly these anomalies could be due to the experiments being conducted in different seas and therefore, in order to confirm the assumptions mentioned above for this particular area, and to obtain a detailed account of the movements of the local plaice population, a series of otolith surveys was carried out from July 1951 to October 1953.

There has been little published work on the movement of inshore plaice since the early 1950s, except for that associated with the project to study the feasibility of fish-farming using hatchery-reared fish, which has naturally been confined to the study of O-group plaice (e.g. Riley 1964, Corlett 1966), although there have been very recent studies of the plaice fishery off Iceland (Bannister, in preparation). It therefore seems worthwhile to present in this paper the results of the otolith surveys of 1951–53 and, insofar as they are relevant to the seasonal movement of inshore plaice, some of the data from the earlier marking experiments.

Equipment and Methods

Most of the otolith surveys were carried out (with the permission of the then Ministry of Supply at Sellafield) on the MARY MUNRO III, a 46 ft motor vessel using a light otter trawl with a covered cod-end, although the RV PLATESSA and several commercial vessels were used in the marking work which preceded them, and some of this information is used in the discussion of the movements of plaice during winter. The MARY MUNRO made short hauls of 1 hour or 1½ hours' duration on a line of stations at right angles to the shore, made up of rectangular strips 1 mile in length and graduated in width from ¼ mile near the shore to 1 mile on the outermost stations. For the purpose of this paper, in Figure 1 the stations are lettered consecutively from A to J, beginning at the innermost rectangle, whose inshore edge is ¼ mile from the low tide level. The depth increases from 4–5 fathoms at station A to about 15 fathoms at station J. Occasionally two extra mile squares lettered K and L, continuing seawards from square J, were fished, but only very small numbers of fish were found.

The bottom is sandy to the east and muddy to the west of the survey area, the 50 per cent mud-sand boundary passing approximately north-south between rectangles F and G. A low ridge of rocks runs parallel to the shore between rectangles C and D, which unfortunately made these two stations impossible to trawl. The centre block of eight 1 mile squares parallel to the shore, shown in Figure 1, is the marking grid used by PLATESSA and other vessels during 1950 and 1951. An Army landing craft towing a 10 ft beam trawl was used to fish the ¼ mile strip immediately inshore of station A in August 1952, because the depth of water was not sufficient for MARY MUNRO.

All species of fish were counted and all plaice were measured, sexed and otolithed, unless the catch was very large, when a random sample of about 100 plaice was otolithed.

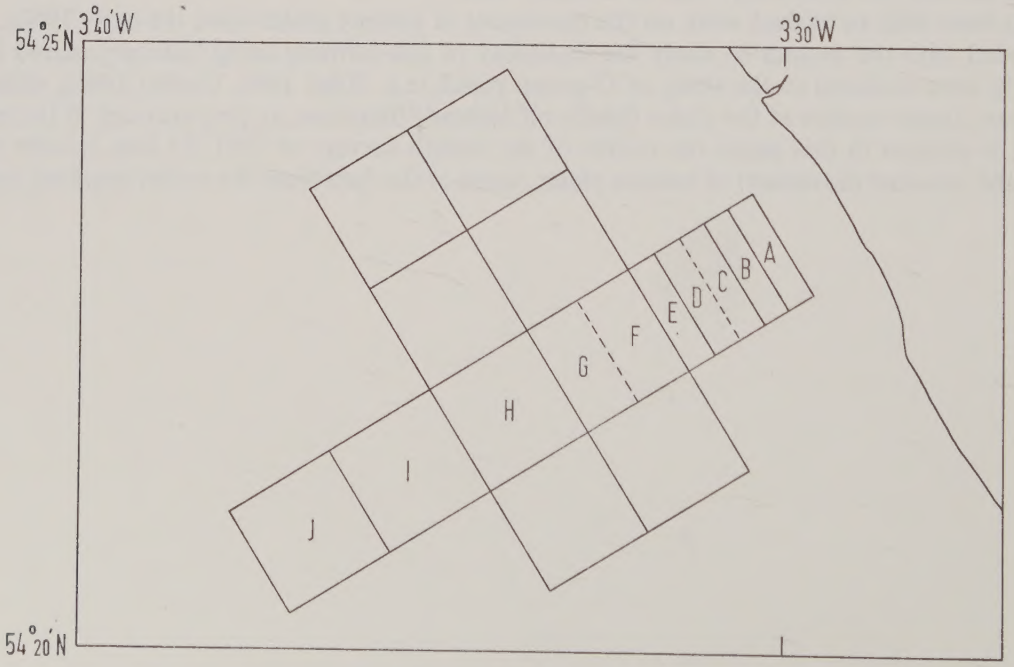

Figure 1 Diagram of the marking grid in relation to the otolith survey stations.

General Results

This investigation was carried out on the edge of a distribution of plaice which spreads over a large area of that part of the Irish Sea between the Isle of Man and Cumberland, and within this distribution, apart from the spawning migrations of the mature fish during the winter, there is in general a random movement of the larger fish.

In the inshore region under consideration, there is a marked contrast in the level of the summer and winter catches. Figure 2 shows the average catch of plaice per hour during 1950, 1951 and 1952, the three years for which there was complete coverage in the marking grid shown on Figure 1. In general the catches are very low during the winter, but there is a slight increase at the end of February and during March, after which they build up very quickly at the end of April and the beginning of May. Considerable numbers are caught throughout the summer until the end of October, and by the end of November they are down to the winter level, the decrease in catch in the autumn being more gradual than the increase in April and May. This annual appearance and disappearance of the fish and its timing agrees with that summarized by Wimpenny (1953) for the North Sea, and various workers have suggested that it is temperature-controlled. Certainly, in this part of the Irish Sea the most rapid rise and fall of sea temperature occurs at approximately the same time as the appearance and disappearance of young plaice from the coastal waters, the difference in monthly mean temperature at the Solway lightvessel (which is the most relevant station at which long-term records have been taken) being 3.2°C between April and May, and 3.64°C between October and November, out of a total rise and fall in monthly mean temperature of 11.04°C (Bowden 1955).

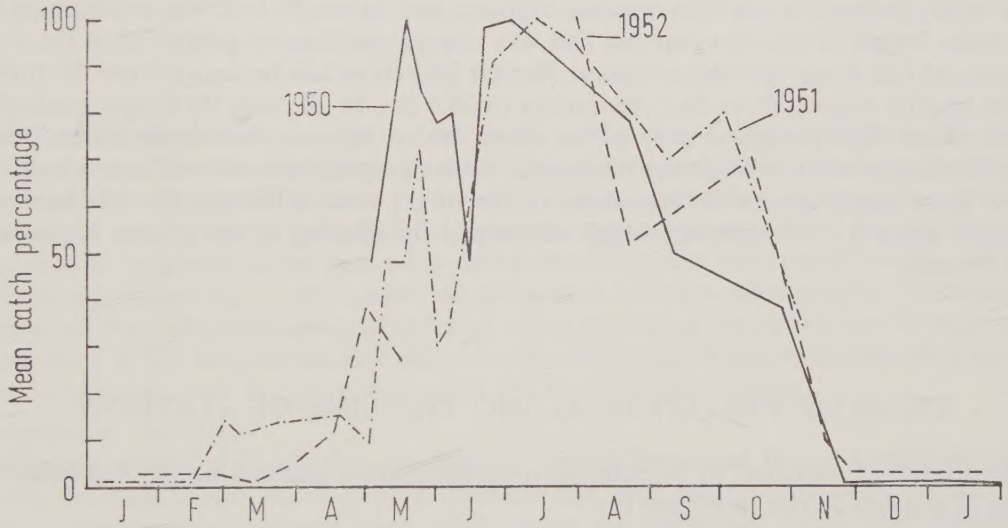

Figure 2 Mean catch of plaice per hour in the years 1950, 1951 and 1952. (The scale of the ordinate has been adjusted so that the maximum catches are shown as 100 per cent.)

On two occasions during the summer months exceptionally low catches occurred; these have been excluded from Figure 2. On 25 June 1952 and on 28–29 June 1951, very small numbers of plaice were caught not only in the marking area but all along the line of stations. In both years these catches averaged only 16 per hour over a number of hauls, against an expected catch of 90 or 100 per hour. There are two possible explanations. Either there had been a general offshore movement of all age-groups, or the fish were for some reason less catchable at that time. The evidence supports the latter alternative, since:

(a) the percentage composition of the catch along the line of stations remained as expected from the cruises before and after the low catches;

(b) the mean length of fish at the outer stations did not increase; and

(c) those who marked the fish at this time of year reported that the general condition of the fish was very poor. Further evidence of this is given in Table III of the Appendix which shows the total returns of plaice marked at different seasons throughout 1949. It is seen that the returns for fish marked from 30 June to 2 July were only about one-quarter of the average, indicating a high mortality at the time of marking.

If, then, the fish were sluggish and lifeless and hence did not "rise" to the groundrope on the occasions in June when such small numbers were caught, the total catch would of course decrease, but the age and size composition of the catch would remain the same.

GRADING BY LENGTH AND AGE-GROUP

The fish were found to be graded by age, and by length within age-groups, as well as the more obvious and often reported grading by length irrespective of age, the oldest and largest tending to be found furthest offshore. Typical examples are shown in Tables I and II of the Appendix for the surveys carried out between 30 April and 2 May 1952, and on 15 May 1952. The mean length of one-year-old plaice varied from 9.3 cm at station A to 15.5 cm at station F on the former survey and from 9.6 cm at station A to 17.5 cm at station E on the latter, the size of the fish tending to increase uniformly with distance offshore, and hence with depth, although the sample sizes were very small at the outer stations. Similarly, within the II-group distribution, the mean length increased from 17.2 cm at station A to 19.9 cm at station H on the first of the surveys, and from 17.2 cm at station A to 20.4 cm at station G on the second; this shows a reasonably steady increase in size with distance offshore, and although there was overlapping of the age-groups, the mean length of the two-year-old fish was always significantly greater than the mean length of the one-year-old fish at any particular station. Similar inferences can be drawn from the three-year-old fish, the mean lengths ranging from 20.1 cm inshore to 26.5 cm. In all cases the length grading within an age-group was more clearly marked near to the shore, which suggests that depth rather than distance offshore was the predominant factor, since the depth increased rapidly between stations A and E, and then shelved rather more gently across the remainder of the survey area. Although the fish were also clearly graded by length alone (i.e. irrespective of age) with depth, the grading by age-groups appeared to be the more clearly defined.

TYPES OF VARIATION ALONG THE LINE OF STATIONS

There are three types of variation to be taken into account when interpreting the movements of plaice along the line of stations shown in Figure 1:

(i) "*Between cruise*" *variation*

There may be high (or low) catches on all stations, due to the condition of the fish, as discussed above. This may also be caused by some factor prevailing throughout the cruise, such as the state of the sea or, according to local fishermen, an onshore wind.

(ii) "*Between station*" *variation*

During the summer the catches are very high close to the shore and tail off rapidly further out. This is partly due to a gradual change in the bottom from fine sand to smooth mud, since the fish tend to concentrate on the sand. Figure 3 shows the PLATESSA's average catch per $1\frac{1}{2}$ hours in the survey area during the period May–June 1951. Two cruises have had to be combined to give complete coverage. Stations A to H and the eight squares of the marking grid were worked at the end of May 1951 and stations F to L

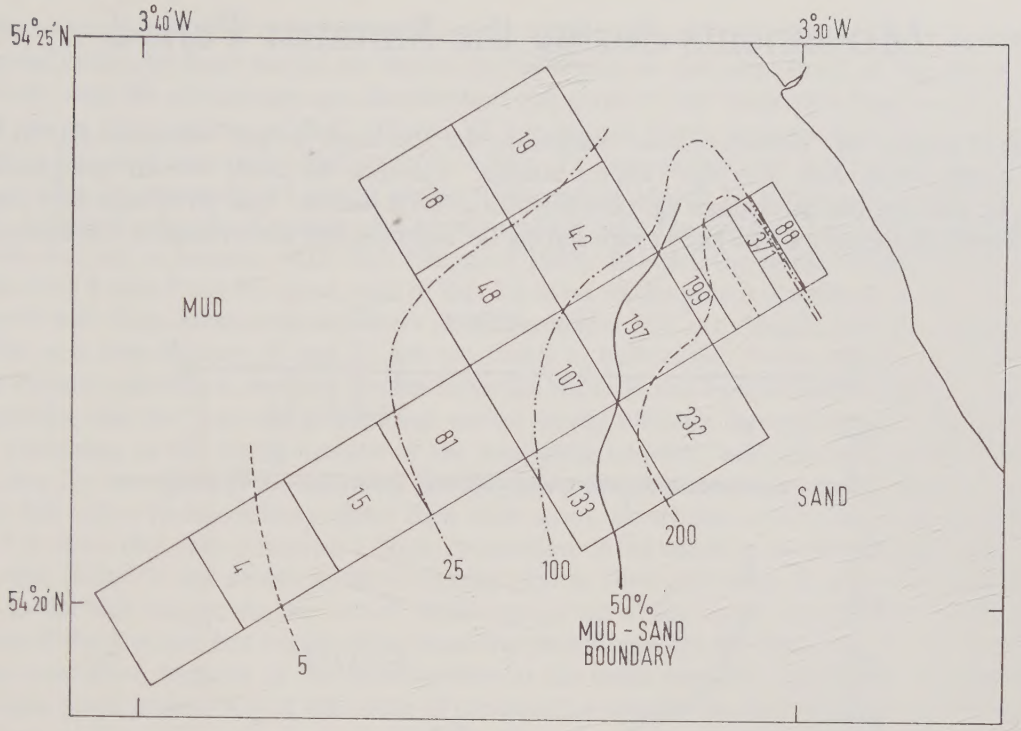

Figure 3 Mean catch of plaice per 1½ hours by PLATESSA over the period May–June 1951.

were fished the following month, i.e. before the cruise at the end of June containing the unusually low catches at all stations. The common stations were then used to scale down the June catches to the May level. This combination of cruise data in Figure 3 gives some indication of the catch contours over the region as a whole, and it can be seen that the contours approximately follow the mud-sand boundary. The catches tend to be higher to the east, where the bottom becomes increasingly sandy, and lower to the west, i.e. diagonally across the survey squares, as the bottom becomes more muddy. This means that there is a component of this bottom-concentrating factor along the line of the otolith survey rectangles, at right angles to the shore. It has been shown that this concentrating factor is due to the changing pattern of food associated with the change of bottom composition (A. Preston, pers. comm.).

(iii) "*Within station*" *variation*

Each of the points shown in Figure 2 is the mean of several hauls and thus the variance about them is small. During the main otolith surveys it was usual to fish each station only once, and hence there is a much greater variance associated with each point. Using the method of Barnes and Bagenal (1951) on PLATESSA hauls in the area, the 95 per cent confidence limits for an individual haul are approximately half and twice the observed value, and hence the expected catch at a station (a true estimate of which could only be obtained by averaging a large number of hauls made over a short space of time) may lie anywhere within these limits. Similarly, any difference in catch between adjacent stations which lies within these limits may not be significant.

Movements during the Summer Period

It is possible to reduce the "between cruise" variation, the "between station" variation due to the change in bottom composition, and also the "within station" variation in catch due to completely random fluctuation, by plotting the percentage age composition at each station. This gives smoother curves which show the offshore movement of the age-groups during the summer, but unfortunately this method conceals

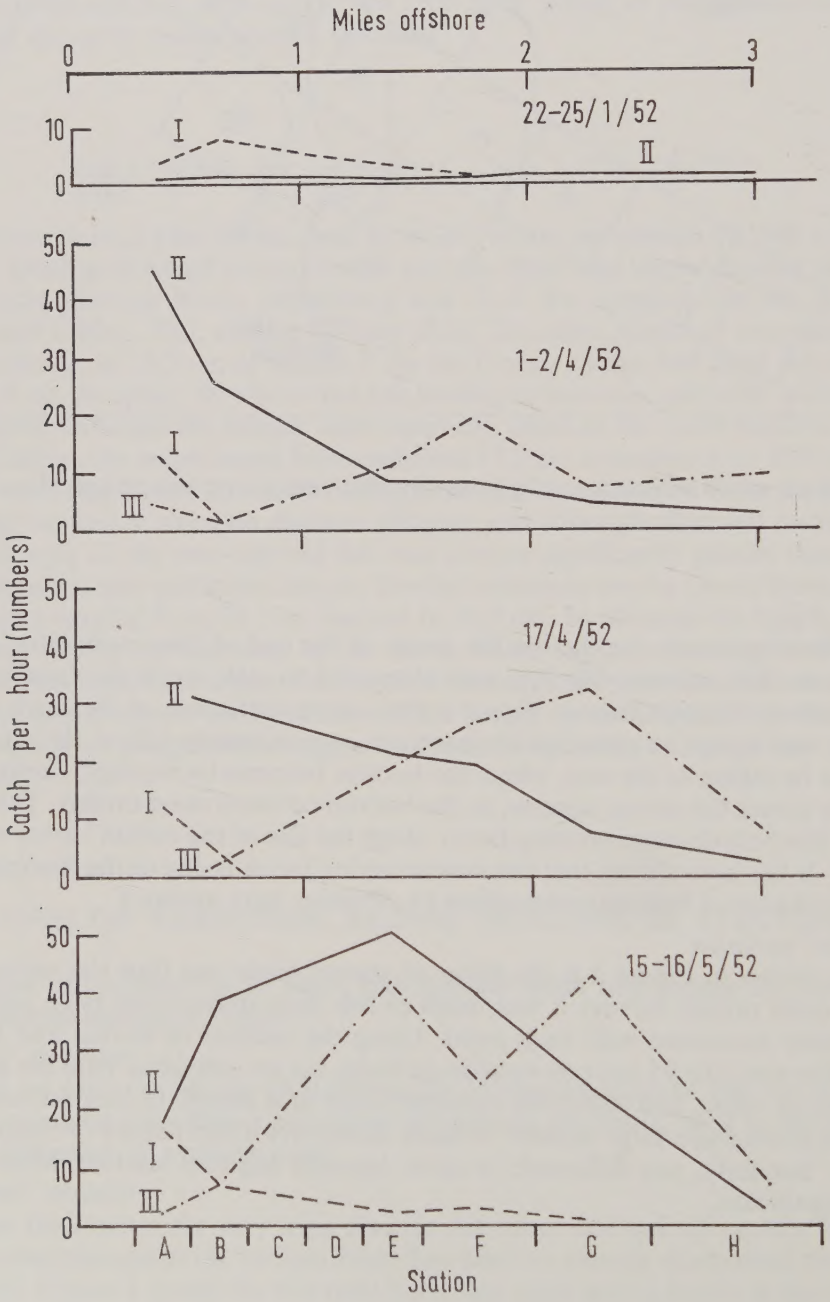

Figure 4 Age-group distributions in January, April and May 1952.

not only the seasonal variation in catch but also any "within station" variation which is significant. Therefore the actual catch per hour curves are shown in the figures in the main body of the paper to illustrate specific points, and the percentage age distributions are given in the Appendix Figures I to IV.

Figure 4 shows the positions of the I, II and III age-groups at the beginning of the year; few IV's are ever caught in this area and older fish are rare indeed. The age-groups are updated at the end of March each year so that, for example, a I-group plaice at the end of March becomes a II-group fish on 1 April. The date is arbitrarily chosen to correspond approximately with the middle of the spawning period, which extends from the end of January until May (Simpson 1959). In April the mode of the I-group distribution is within the first $\frac{1}{4}$ mile from the coast, and in fact for most of the year it is inshore of the line of stations. During April and May substantial numbers of one-year-old fish are caught only at stations A and B, although the next two stations, C and D, are too rocky to be trawled. From the end of July onward, I's begin to be caught regularly at stations further from the shore. It can be seen from Figure 4, and the figures in the Appendix, that the II-group distribution moves slowly offshore throughout the spring and summer, the mode appearing in the inner stations at the beginning of May, and this year-group is spread right across the area for the whole of the summer. The III-group distribution is seen from Figure 4 to be building up as more fish arrive from offshore where they have spent the winter as II's, and from the figures in the Appendix it is clear that they comprise a large proportion of the catch in the first 4 miles until the middle of the summer. They do not return in the following year as four-year-olds. It should be remembered that the figures in the text exaggerate the cut-off of the age-group at the outer stations due to the effect of the composition of the bottom, but on the other hand the percentage age distributions shown in the Appendix have the reverse effect, because of the small catches at the outer stations. Obviously, since three-year-old fish make up a good proportion of the catch of commercial trawlers in the Irish Sea throughout the year, and two-year-old fish contribute from about July, the tails of the distributions of these two age-groups are not limited to the region under study.

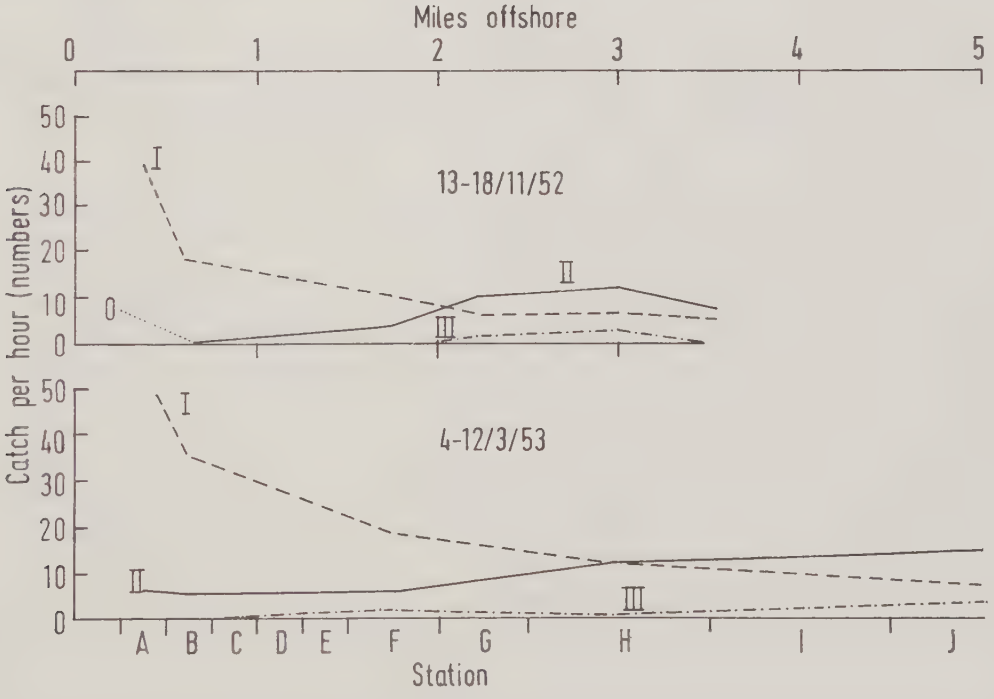

Figure 5 Age-group distributions in November 1952 and March 1953.

Figure 5 shows the positions of the age-groups at the end of the summer period, in November. The inshore tail of the II-group distribution is still visible but most of the group has moved offshore. The III-

group has already moved to deeper water—very few of them are caught inshore at this time of year. A few of the larger and more mature I's leave to winter offshore but the majority still remain close inshore. At all stations during the winter the catches are very low, but there were always more I-group caught on the inner stations than on the outer ones. Hence those I-group which do remain inshore stay relatively in the same position as they occupied during the late summer. The O-group stay within the first $\frac{1}{4}$ mile from the shore until the autumn, when a few are caught at the inner stations. In order to verify that they were in fact there during this time, an Army landing craft was used to tow a 10 ft beam trawl in the shallow water close to the shore in August 1952, and large numbers of them were caught. A few O-group plaice were also found in the sandy pools left on the shore as the tide receded. On only one occasion did this group appear on the inner stations in any numbers; this was during the cruise from 19–27 February 1952, at the end of the winter, as they were about to become the I-group of the next spring.

Figure 5 also shows that as the fish begin to re-appear in March they appear in very much the same positions as at the end of November, and by comparison with Figure 4 it can be seen that the I- and II-groups are in the positions that the II- and III-groups occupied the previous April.

FINER STRUCTURE OF THE OFFSHORE SUMMER MOVEMENT

The positions of the age-groups move slowly offshore during the summer, but this movement is small compared with the area over which the large fish are dispersed, and it cannot be called "a migration" in the sense of the winter spawning migration. However, it is worthwhile to consider the positions, and in particular the shape of the distributions, in more detail. Figure 2 shows a drop in catches at the end of May and the beginning of June over the marking grid which overlaps stations F, G and H. Figures 4 and 6 show the II- and III-groups spread well across the line of stations in the middle of May in 1952 and 1953. The variations in catch here are within the 95 per cent confidence limits. However, on 9 June 1953 there were heavy catches inshore which were significant, and which suggest a short but transient inshore movement at this time. A similar phenomenon was observed at the end of May 1951. Unfortunately there was no fishing at this time in 1952, but there is further evidence of a slight reversal of the general trend from the recaptures of marked fish released from PLATESSA in May and June 1950.

In these two months fish were marked, released and later recaptured on successive cruises in each of the eight one-mile squares of the marking grid shown on Figure 1. The numbers of recaptures per 10 hours' trawling are shown in Table 1, totalled for the inshore and offshore rows of squares, which may conveniently be termed the FG and H rows. Recaptures from the last three cruises are combined since the numbers are small. The recaptures are comparable across the rows of the table but not from cruise to cruise down the columns. It is clear that there are more recaptures inshore on the first two cruises, in the last half of May, and that by the beginning of June they are about equal, i.e. there appears to have been an inshore migration at the end of May, similar to that described above.

There is no obvious oceanographic or meteorological anomaly with the appropriate timing which might suggest a reason for this apparent transient reversal of the general slow movement offshore of the age-groups during the summer months, but the fact that there is evidence of its occurrence in all those years in which the relevant areas were fished suggests that it is real. A colleague has suggested that the reversal could be due to the breakdown of the winter negative thermocline which exists in these inshore waters (A. R. Folkard, pers. comm.).

During the winter, the surface water is colder than the bottom water, with the thermocline at about 7–8 fathoms. By April, just before the most rapid rise in water temperature mentioned earlier, the temperature along this negative thermocline is about 6°C, so that at the inner stations of the survey grid the water is not only well mixed from top to bottom, and less than 6°C, but it is also subject to diurnal fluctuation, reaching considerably colder temperatures during the night. It might reasonably be presumed that the majority of the fish tend to keep to the warmer water below the thermocline at this time. However, as the water temperature rises, the temperature profile reverts to the normal summer condition in which the surface water is warmer than the bottom layer. For example, Jones and Folkard (1971) showed that

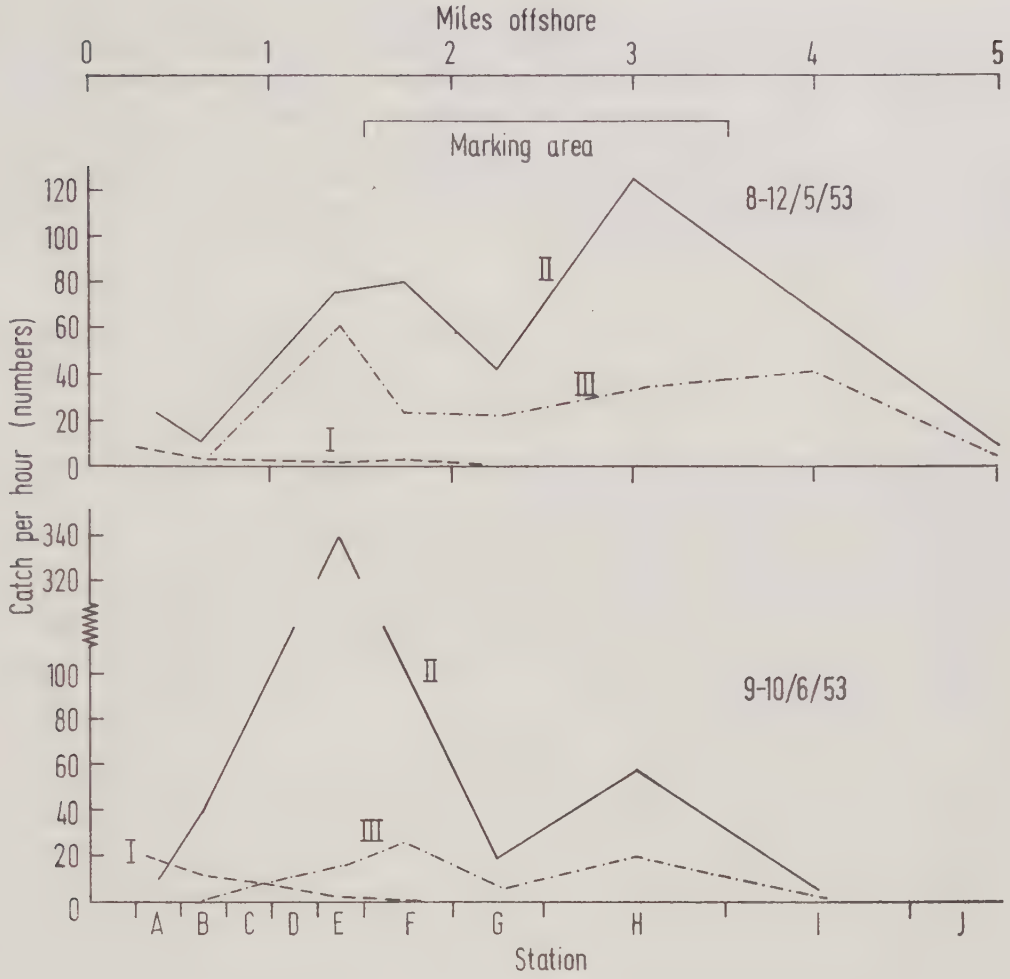

Figure 6 Age-group distributions in May and June 1953.

Table 1 Recaptures in inshore (rows FG) and offshore (row H) areas of marked fish released in the period May–June 1950 (numbers per 10 hours' trawling per 1 000 fish released)

Date of cruise	Released in FG row		Released in H row	
	Recaptured in FG	Recaptured in H	Recaptured in FG	Recaptured in H
16–20 May	17.8	8.4	15.0	6.9
22–25 May	4.2	0.9	14.1	4.5
31 May–2 June	2.8	2.3	9.9	10.1
5– 8 June 12–15 June 19–23 June	3.5	4.6	3.8	4.1

in June 1967 there was a sharp thermocline off St Bee's Head, temperatures rising to 11 °C on the surface, and falling to about 9 °C on the bottom. Between these two states there must occur a short period, at approximately the time of the reversal in offshore movement, when the negative thermocline breaks down and relatively warm water spreads inshore over the bottom, and the fish, if they have tended to be limited to this warmer water, would move in with it. This does not of course explain the transient nature of the reversal, since the bottom temperature continues to increase thereafter at the inshore stations, but it is suggested that the fish may become temporarily confused by the spread of the warm water and subsequently revert to the other conditions to which they have become adjusted, such as the depth of water or the availability of suitable food.

MATURITY GRADING IN AUGUST

In August 1952 two maxima were observed in the II-group distribution at stations E and I, as shown in Figure 7; the outer one, at least, is greater than would be expected from purely random variation. If it were due to a good patch of feeding at this distance from the shore, high catches would be expected there over a longish period; this did not in fact occur. It has already been shown that plaice do tend to be graduated by lengths within an age-group—the smallest being near the shore. However, a study of the length distributions at the two stations revealed no unexpected differences, and furthermore, the ratio of the sexes was the same at both stations. At the beginning of October, there was again a suggestion of a split in the II-group distribution.

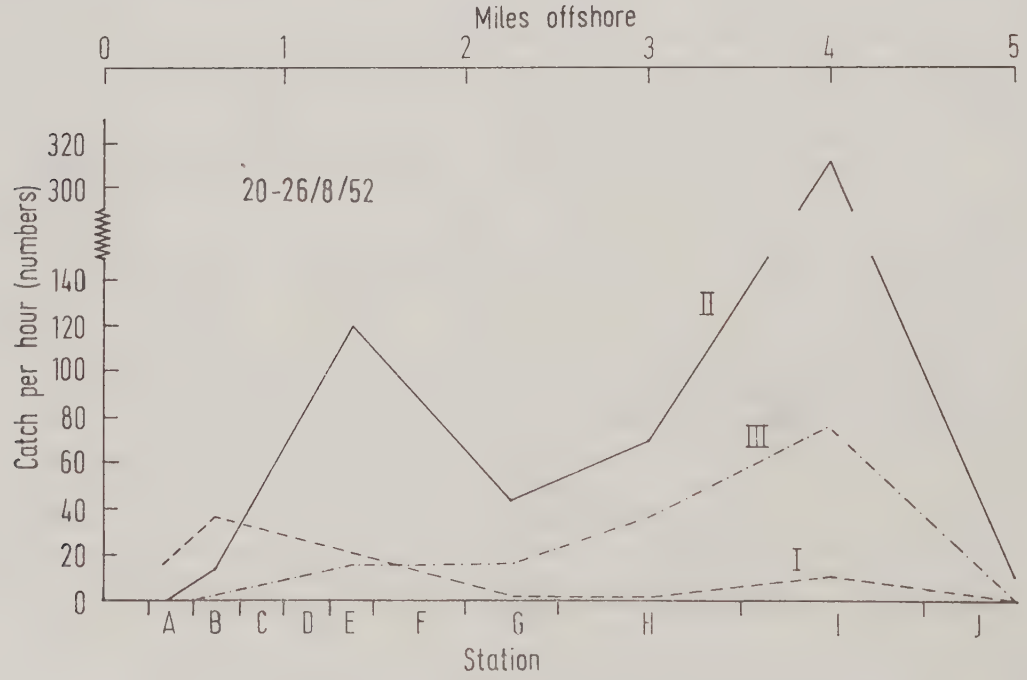

Figure 7 Distribution of age-groups during the period 20–26 August 1952.

Since it was already known that fish spawn at an earlier age in the Irish Sea than in the North Sea, and that many of the two-year-old males would be fully mature by the winter, it appeared that the more mature individuals might be accumulating at the outer edge of the distribution in August. Similar maxima were again found at the same stations in August 1953, and on this occasion samples of large (>23 cm) and small (< 23 cm) plaice of each age-group were taken from each station where the maxima occurred and also from an intermediate station, G. These fish were measured, sexed and otolithed and the gonads were weighed fresh. The mean weights of the gonads of fish of similar length groups are shown in Table 2.

Table 2 Mean weight of plaice gonads at stations E, G and I in August 1953 (in grammes)

Age and size	Sex	Inshore station E		Intermediate station G		Offshore station I	
		Mean	Range	Mean	Range	Mean	Range
II small	Female	0.252	0.19–0.35	0.382	0.31–0.45	0.414	0.26–0.59
	Male	0.027	0.02–0.03	0.035	0.01–0.06	0.062	0.05–0.08
II large	Female			0.780	0.51–1.35	0.850	0.73–1.08
	Male			0.064	0.05–0.08	0.083	0.07–0.10
III large	Female			1.048	0.55–1.58	1.314	0.84–1.75
	Male			0.140	0.08–0.29	0.240	0.16–0.30

It is clear that for fish of the same size and age, the gonads are heavier at the offshore station, and hence we may conclude that the two- and three-year-old fish of both sexes are more mature, size for size, the further they are offshore. Therefore, it would seem that there is some evidence that a grading by maturity exists within the age groups, and from Figure 7 it would appear that the more mature fish congregate towards the outer edge of their parent distribution at the end of August prior to moving off to the spawning areas. Unfortunately, there were not enough one-year-old fish at the outer stations to allow a comparison to be made for this age-group, nor enough two- or three-year-old fish to provide representative samples at station E, but it is possible that even among the one-year-old fish there might be a difference in maturity at this time. Simpson (1959) found one-year-old mature males as small as 16 cm in length just off this area in February 1953, and on the present survey one-year-old females were caught with gonads weighing up to 0.18 grammes, whereas the more representative weight for this age-group varied from 0.03 to 0.08 grammes.

Position of the Age-groups during Winter

In the inshore region under consideration, the catches are extremely low from the end of November until the beginning of March. Only the O- and I-groups are caught in reasonable numbers, at about one-tenth of the summer level, and then only very close to the shore. The modes of these two year-groups are never seen further out than the first mile, but the II- and III-group modes are seen to move right out of the area. Wimpenny (1953) refers to this apparent disappearance of the fish as the "winter dig-in", quoting similar reductions in numbers at this time in other areas and suggesting that the fish bury themselves too deeply to be disturbed by the groundrope of a trawl.

Some idea of the extent over which the two- and three-year-old fish have spread and the positions of these age-groups in the winter can be obtained by looking at the commercial returns of marked fish during the winter months. In October 1950, 2 300 plaice were marked on the PLATESSA; the area over which they were recaptured during the winter is shown in Figure 8. Unfortunately the details of the fishing effort are not known accurately for this period. Hence the distribution of fish shown in Figure 8 is not corrected for effort and does not necessarily show the true spread of the marked population. However, it is valid to compare the proportions of age-groups or sexes within annuli at different distances from the point of release, and this gives an indication of the distribution of the age-groups and sexes over the area of recapture.

COMPARISON OF SPREAD OF AGE-GROUPS

During November, the inshore population is decreasing in number. Therefore, recaptures during November from releases the previous month should give some indication of the way in which the fish are graded during the latter part of the move offshore. The area over which the marked fish were recaptured in November is very similar to that for the following three months as shown in Figure 8, but also includes the area of the Selker fishery. This commercial fishery lasts from April until November and is in many respects the commercial counterpart of the area in which the otolith survey was carried out.

It can be seen clearly from Table 3a, without a statistical test, that in November the II's and III's are in the same proportion over the whole region, and hence it may be assumed that there is no difference during this month in the dispersal of the age-groups of those fish that are large enough to be marked. (In fact $X^2 = 1.90$, which is not significant at the 10 per cent level with 3 degrees of freedom, columns 4 and 5 being combined.) The recaptures of I's and IV's also bear out this hypothesis. Figure 5 shows that at this time the I's are still inshore as a group, but in this inshore region only those one-year-old fish which are too small for marking, i.e. less than about 18 cm long, are represented. Thus, of those fish which do go offshore for the winter, there is no significant difference in dispersion by age, as occurs during the summer in the inshore areas.

It can be seen from Figure 8 that the recaptures taken during December, January and February from fish released in October are all from approximately the same area, but that the area is very different from the area of recapture of those fish marked in April of the same year. The numbers are too small to consider these months separately. In Table 3b, the first segment (0–8 miles) corresponds roughly to the area under consideration during the summer period. The 16–24 mile bracket includes the Bahama Bank winter fishery, which accounts for the larger numbers.

In fact, less than 4 per cent of the recaptures during the period December–February were caught more than 32 miles from the point of release. The ratio of the two-year-old to three-year-old fish is fairly constant—certainly up to a radius of 24 miles. In order to test whether these ratios are different from the expected values, columns 1 and 2 and columns 4 and 5 of Table 3b are combined, since, for the X^2 test to be valid, the cell frequency should not be less than 5. This gives a value of $X^2 = 1.67$, with 2 degrees of freedom, which is less than the 10 per cent level and therefore not significant, and hence it may be concluded that there is no difference in the spread of the II- and III-year groups. The few recaptures of I's

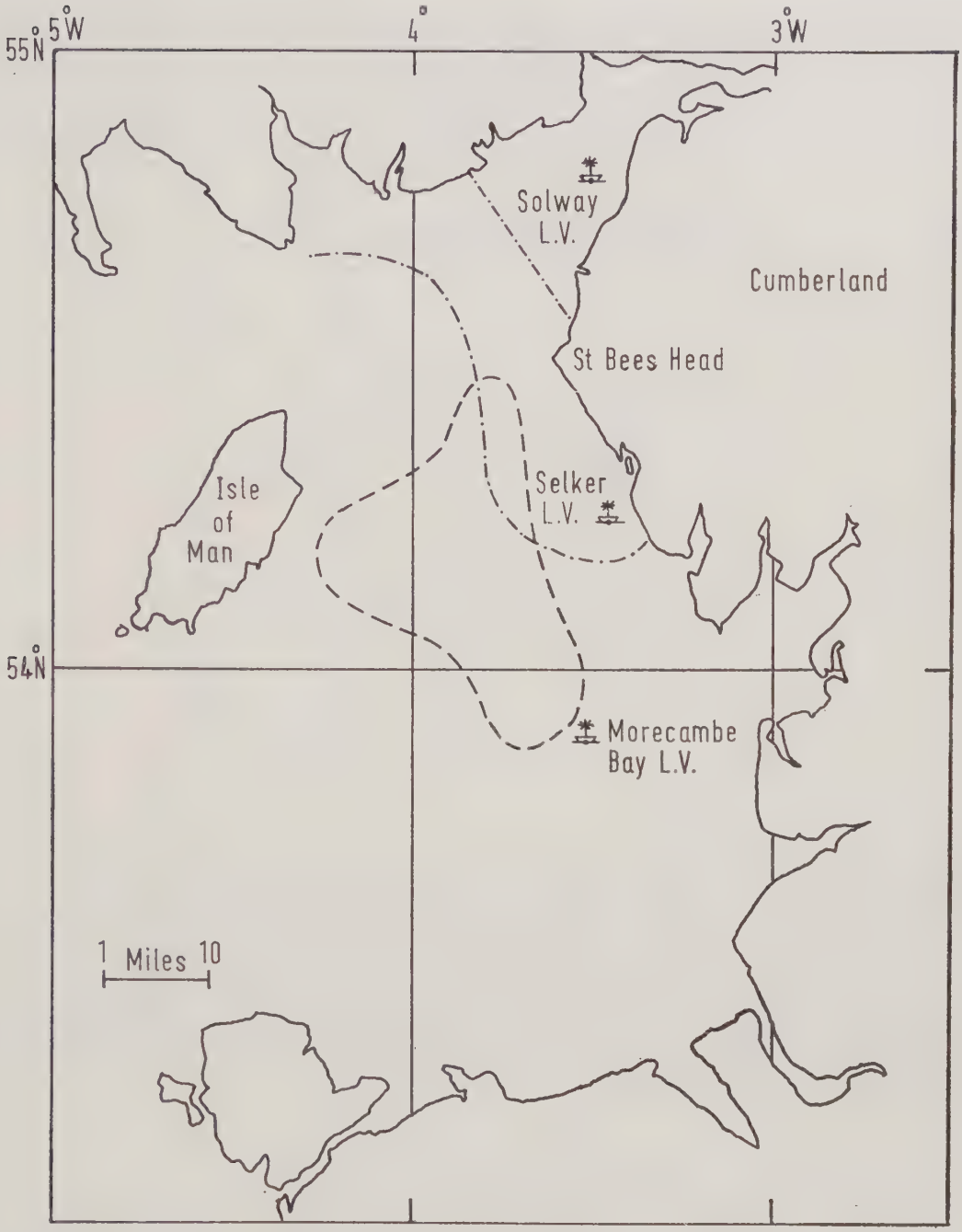

Figure 8 Chart of the areas of recapture of fish marked in the grid shown in Figure 1.
· — · — · — May and June recaptures of fish released in April.
— — — — — December–February recaptures of fish released in October.

and IV's lend further support to the conclusion that the age-groups are spread randomly with respect to age over the area of recapture during the winter months, since the older fish were caught close to, and the younger fish farther away from, the release area, which is the reverse of what would otherwise be expected.

By March, the fish are beginning their inshore spring migration. The recaptures taken during this month from the October 1950 release suggest, in Table 3c, that the fish are then arranged in the order which they assume during the summer on their return to the inshore grounds. In this table there are sufficient numbers

Table 3 Comparison of age-groups among recaptures of marked fish from the October 1950 releases

Age-group	Miles from release point					Totals
	0–8	8–16	16–24	24–32	>32	
	(a) Recaptures taken in November 1950					
I	5	0	5	1	1	12
II	23	5	18	4	2	52
III	47	13	25	12	2	99
IV	3	0	2	0	0	5
	(b) Recaptures taken in December 1950 to February 1951					
I	0	0	2	1	0	3
II	9	1	24	5	2	41
III	9	3	26	14	1	53
IV	1	0	0	0	0	1
	(c) Recaptures taken in March 1951					
I	0	1	0	0	0	1
II	1	10	4	8	2	25
III	0	13	22	18	15	68
IV	0	0	0	1	1	2

in each cell to test the proportion of II's against III's in a 2×2 contingency table, if the first two and last three columns are combined, X^2 being calculated as 4.68, which is significant at the 5 per cent level, with 1 degree of freedom. It may therefore reasonably be concluded that, at this time, the distribution of the three-year-old fish is spread significantly further offshore than that of the two-year-olds. The impression given in Table 3c, that the fish are recaptured further away from the point of release in March, may be a reflection of a change in fishing effort. On the other hand, very few of the III's are seen back in the marking area as IV's, and they may be beginning a further diffusion, but conclusive evidence on this point would need further study and is beyond the scope of this paper.

COMPARISON OF SPREAD OF SEXES

When the fish are migrating offshore in November there are significantly more males than females inshore. This is shown by considering the ratio of males to females in Table 4a, where the ratio is reversed for the annuli greater than 16 miles, and when tested in the 2×2 table obtained by combining the first two and last three columns, $X^2 = 4.69$, which is greater than the 5 per cent level of significance, using 1 degree of freedom. Since the fish were all released together at the same position, this means that of the fish present in October, the females move out more quickly than the males, presumably because they mature earlier. An examination of Table IV in the Appendix shows that this is more noticeable among the II's than the III's. After November, at the end of the move offshore, this relatively larger proportion of males inshore no longer shows from the recaptures, and for the period December–February Table 4b shows no significant difference in the dispersion of the sexes ($X^2 = 1.95$, which is not significant at the 10 per cent level

with 2 degrees of freedom for the 3×2 table formed by adding together the recaptures in the first two columns and last two columns to obtain frequencies large enough to make the test valid).

In March considerably more males than females were recaptured for the first time, and Table 4c suggests that there was a relatively larger proportion of males offshore, although the X^2 test showed that this apparent difference was not significant ($X^2 = 3.35$, which is not significant at the 10 per cent level for the table formed by summing the first two columns).

Table 4 Comparison of sexes among recaptures of marked fish from the October 1950 releases

Sex	Miles from release point					Totals
	0–8	8–16	16–24	24–32	>32	
	(a) Recaptures taken in November 1950					
Male	42	10	19	6	1	78
Female	36	8	31	11	4	90
	(b) Recaptures taken in December 1950 to February 1951					
Male	6	1	25	9	1	42
Female	13	3	27	11	2	56
	(c) Recaptures taken in March 1951					
Male	0	14	14	21	12	61
Female	1	10	12	6	6	35

DISCUSSION

Thus we can summarize the spread of the fish in the period November–March as follows:

(a) there is no significant difference in dispersion by age from November to February, but by March they are assuming the order of the inshore populations in the summer—the youngest nearest the shore; and

(b) the females (especially among two-year-olds) move more quickly offshore in November, but this difference in dispersion is not maintained throughout the winter.

In contrast, fish released in April 1950 at the beginning of the summer, and recaptured over the region shown in Figure 8 during May and June, showed that the three-year-old fish disperse more quickly and over a larger area than the II's, which are mostly still too close to the shore to be heavily fished by commercial vessels. This is shown in Table V of the Appendix, which gives the number of recaptures by age-groups, during May, June and July, of fish released in April. By July, however, all age-groups appear to have attained the same spatial distribution, but it should be remembered from Figure 8 that the fish have tended to move laterally along the coast towards the Solway Firth at this time of year, and therefore the distances from the release point do not represent the degree of movement into deeper water offshore that was shown in the early months of the winter after the October releases.

The sexes also appear to behave differently over this region in the early summer, in that there appears to be little difference in their rates of dispersion after release, as is shown by Table VI of the Appendix, which compares the recaptures of males and females released in April and caught at various distances from the release position in May, June and July.

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Appendix Table I Length distribution by age-groups, 30 April–2 May 1952

Length group (cm)	Rectangle														
	A			B		E		F			G		H		
	Age-group														
	I	II	III	II	III	II	III	I	II	III	II	III	II	III	
7– 8	4														
8– 9	6														
9–10	10														
10–11	5														
11–12		2													
12–13	1	3				1									
13–14		3						1							
14–15		1		1		1		1							
15–16		6		2											
16–17		16		1				1	6	1	1		1		
17–18		18	2	5		4		1	11		4	1	7	1	
18–19		10	2	8	1	5	1		13	2	11	1	5	3	
19–20		12	2	8	1	3			12	3	12	2	11	4	
20–21		5	2	3	4	2	3		4	2	5	4	5	8	
21–22				5	9	1	1		2	6	4	5	3	5	
22–23			1	6	9		7		1	10	3	5	7	9	
23–24			2	1	9	1	1			7	1	4	1	7	
24–25					12		3			5		2		11	
25–26					8		1		1	4	1	4	1	12	
26–27					6		1			7		6		10	
27–28					3		1			3		4		4	
28–29					2							3			
29–30					1					3		1			
30–31							1			2					
31–32							1								
32–33														1	
33–34															
34–35										2					
Mean	9.3	17.2	20.1	19.5	23.9	18.6	23.7	15.5	18.8	24.2	19.8	23.9	19.9	23.6	

Appendix Table II Length distribution by age-groups, 15 May 1952

Length group (cm)	Rectangle																				
	A			B			E					F					G		H		
	Age-group																				
	I	II	III	I	II	III	I	II	III	IV	V	I	II	III	IV	V	II	III	II	III	IV
7– 8	1																				
8– 9	8			1																	
9–10	6			1																	
10–11	7	1		5																	
11–12	3	1		3								1									
12–13		1		1																	
13–14					2							1	1								
14–15		1			1																
15–16		1										1	1								
16–17		5			13	1	1	3					1				1				
17–18		4			8		1	5	1				4				1				
18–19		4			12	1	1	19	2				8	1			3		1		
19–20		8	1		11	2		16	6				12	3			9	3	1		
20–21			2		12	3		19	5				10	5			5	2		1	
21–22					1	2		11	6	1			8	4			8	3			
22–23						1		4	10				5	1			3	5			
23–24						1		2	6	1			1	3				14		1	
24–25			1					2	7					3	1		1	10			
25–26			1			1			3					2				8		1	
26–27						1			5					6				6		2	
27–28									2	1				3				4		2	
28–29									1							1		2		1	
29–30									1	1											
30–31									2											1	1
31–32									4	1											
32–33									2		1										
33–34									2												
34–35									2												
35–36											1										
Mean	9.6	17.2	22.1	10.7	18.3	21.3	17.5	20.0	24.6	26.8	34.0	13.5	19.8	23.4	24.5	28.5	20.4	24.3	19.0	26.5	30.5

Appendix Table III Percentage of recaptures by commercial vessels, from successive marking cruises in 1949, up to 20 months after release

Release cruise	% recaptures
March–April	42.2
May–June	50.2
30 June–2 July	11.9
September–October	41.2
November–December	50.9

Appendix Table IV Distribution by age and sex of November 1950 recaptures of marked fish released in October 1950

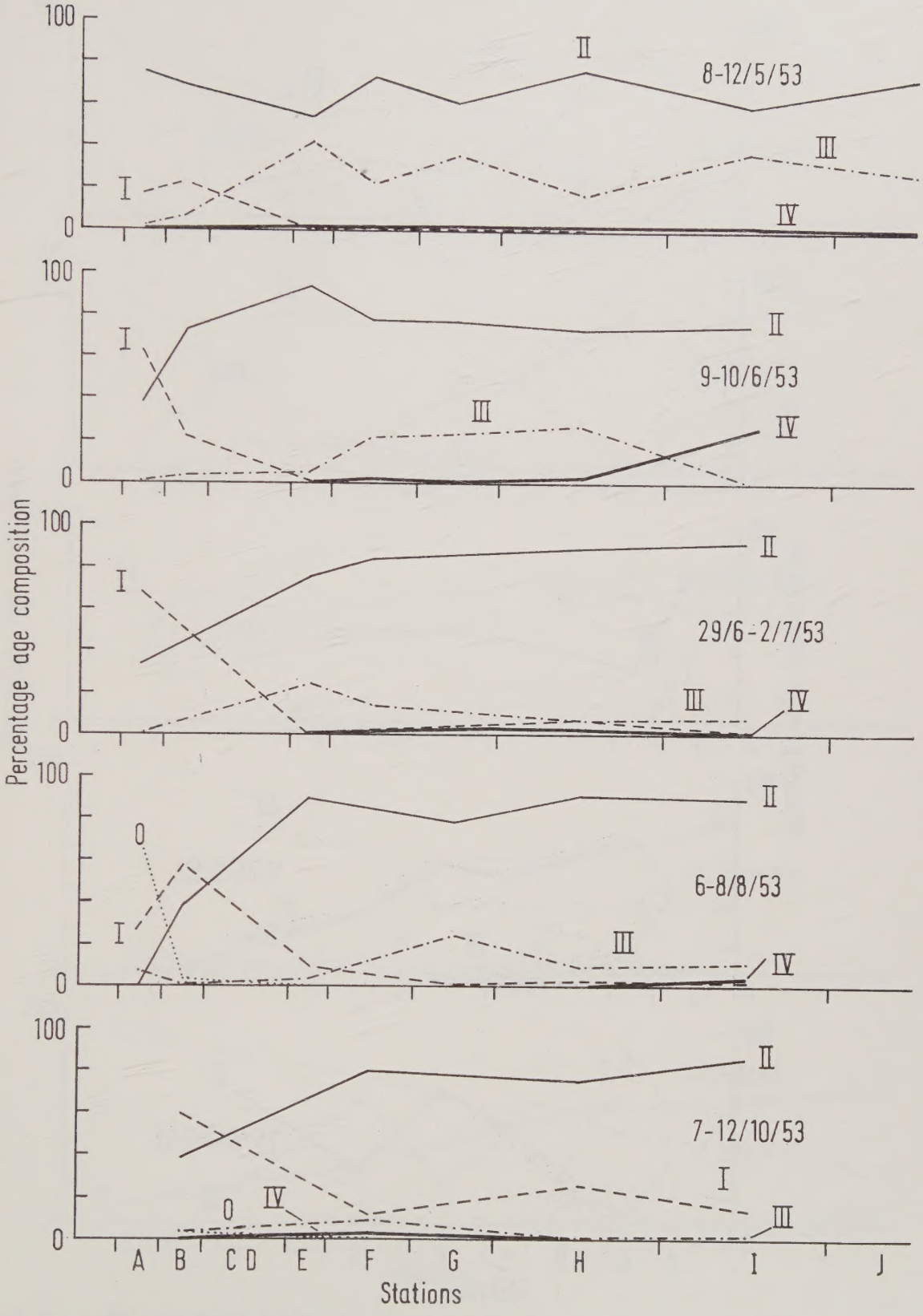
Age	Sex	Miles from release point				
		< 8	8–16	16–24	> 24	Totals
I	Male	4		3	1	8
	Female	1		2	1	4
II	Male	15	4	6	3	28
	Female	8	1	12	3	24
III	Male	21	6	10	3	40
	Female	26	7	15	11	59
IV	Male	2				2
	Female	1		2		3

Appendix Table V Comparison of age-groups for May, June and July 1950 recaptures of marked fish (April 1950 release)

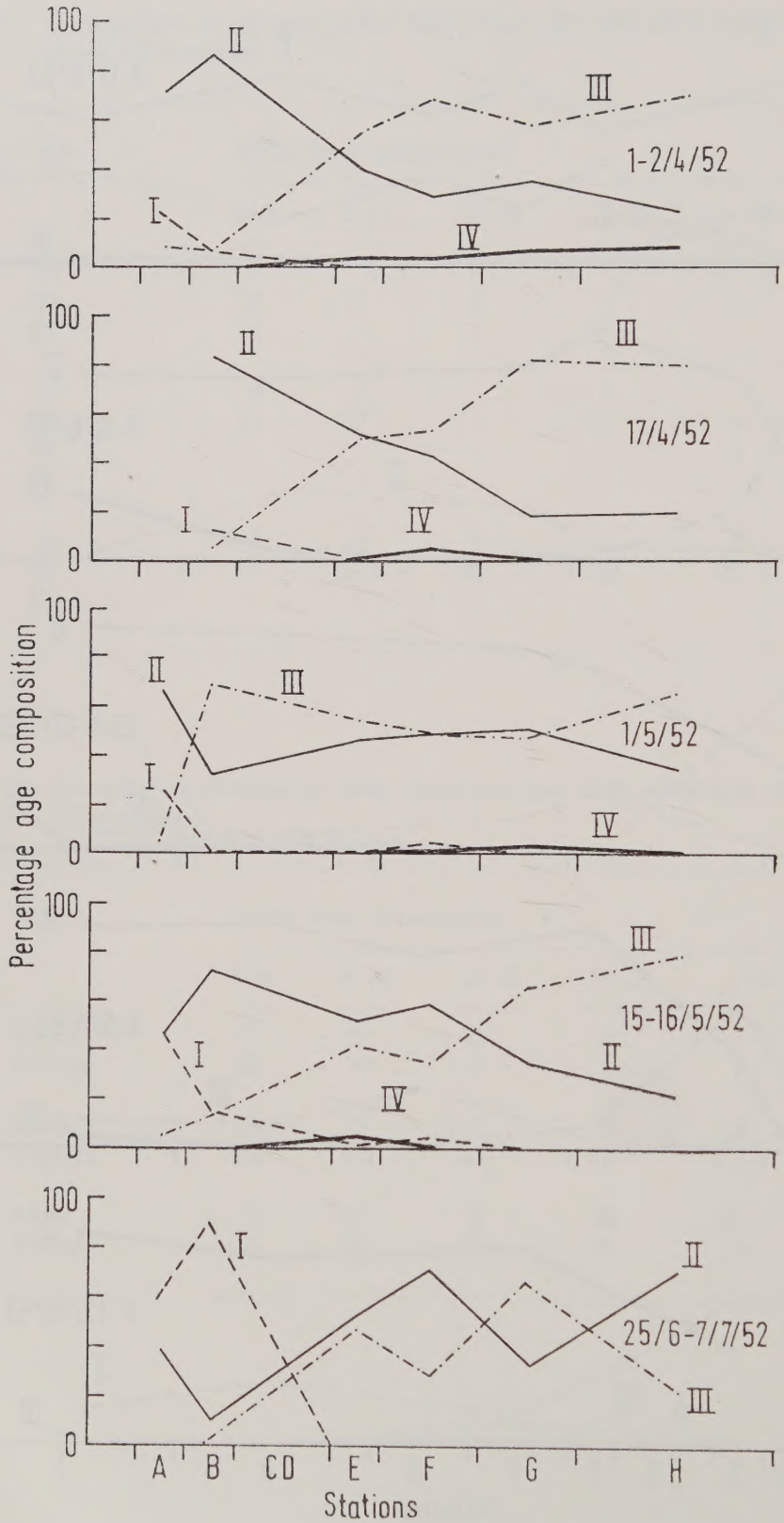
	Age	Miles from release point					
		0–6	6–12	12–18	18–24	>24	Totals
May	II	7					7
	III	22	17	11	3	1	54
	IV	3		1			4
June	II	4	1		1		6
	III	17	27	11	15	4	74
	IV	1				1	2
	V		1				1
July	II	1	4	5	1	5	16
	III	5	23	15	18	18	79
	IV		1		1		2

Appendix Table VI Comparison of sexes for May, June and July 1950 recaptures of marked fish (April 1950 releases)

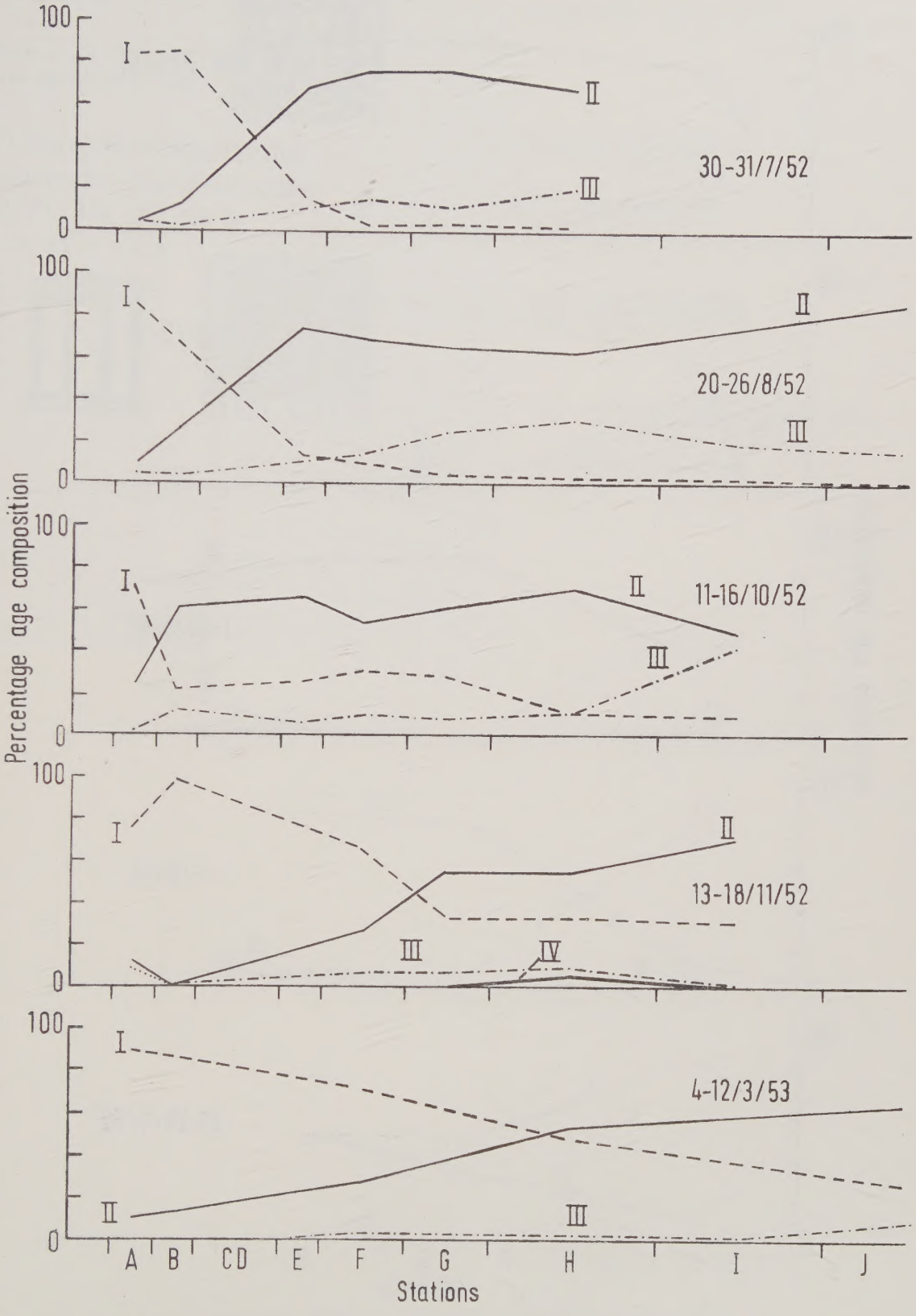
	Sex	Miles from release point					
		0–6	6–12	12–18	18–24	>24	Totals
May	Male	12	9	6	2		29
	Female	20	8	6	1	1	36
June	Male	10	13	7	5	2	37
	Female	12	16	4	11	3	46
July	Male	2	12	8	10	11	43
	Female	4	16	12	10	12	54



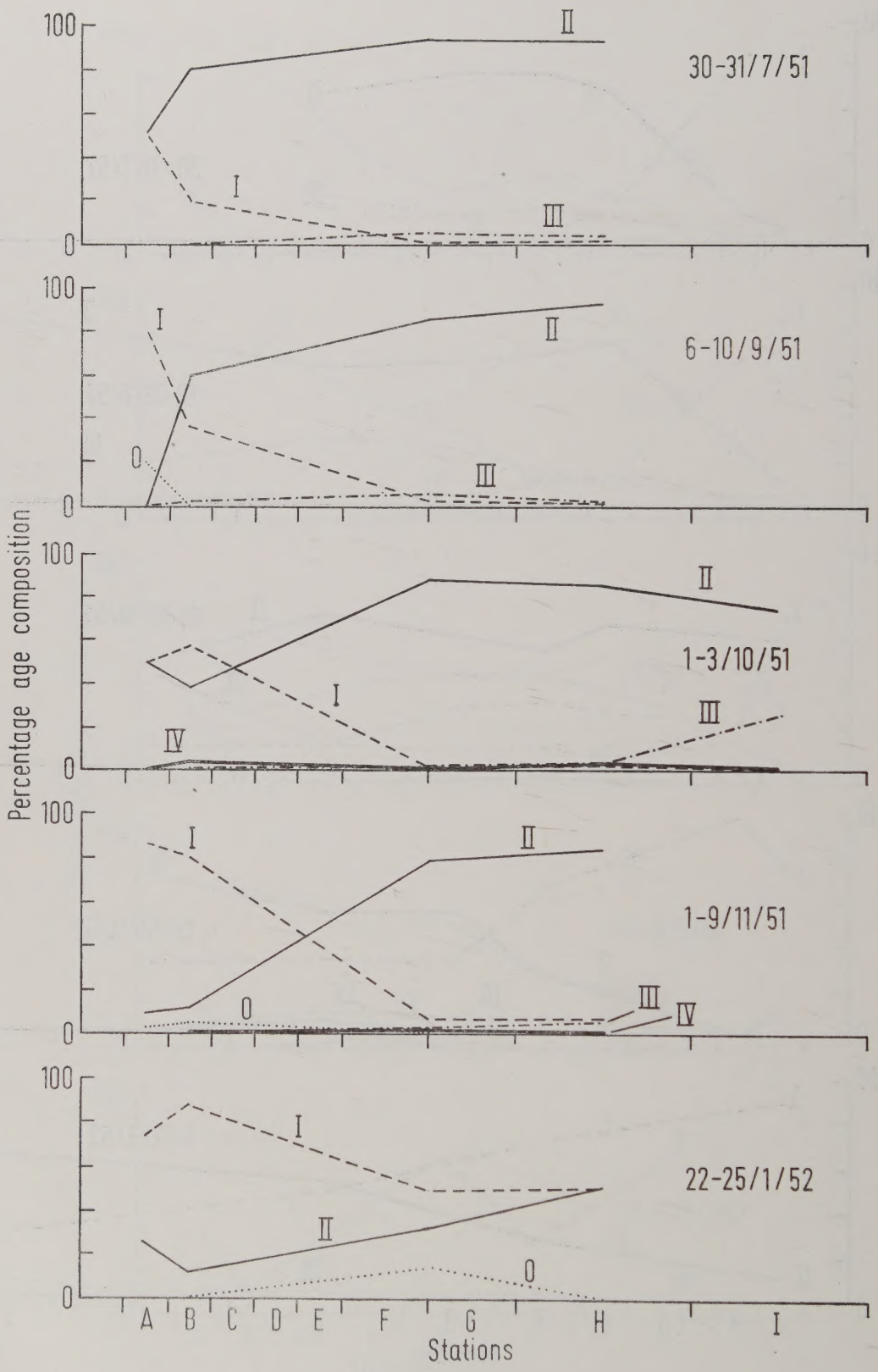
Appendix Figure I Percentage age composition by age-groups, July 1951–January 1952.



Appendix Figure II Percentage age composition by age-groups, April–July 1952.



Appendix Figure III Percentage age composition by age-groups, July 1952–March 1953.



Appendix Figure IV Percentage age composition by age-groups, May–October 1953.

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